

N 9 4 - 1 2 4 5 4

187393

P-12

THE ROLE OF CERTAIN INFAUNA AND VASCULAR PLANTS IN THE MEDIATION OF REDOX REACTIONS IN MARINE SEDIMENTS

MARK E. HINES

Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, NH 03824, U.S.A.

ABSTRACT

The mechanisms by which certain animals and plants affect redox processes in sediments was examined by studying three environments: (1) subtidal sediments dominated by the deposit-feeding polychaete *Heteromastus filiformis*; (2) a saltmarsh inhabited by the tall form of *Spartina alterniflora*; (3) tropical carbonate sediments inhabited by three species of seagrasses. ^{35}S -sulfide production rates were compared to pool sizes of dissolved sulfide and dissolved iron. In all of the sediments studied, rates of sulfate reduction were enhanced by macroorganisms while the rate of turnover of dissolved sulfide increased. The polychaete enhanced microbial activity and redox cycling primarily by subducting particles of organic matter and oxidized iron during sediment reworking. The *Spartina* species enhanced anaerobic activity by transporting primarily dissolved organic matter and oxidants. Although the final result of both animal and plant activities was the enhancement of sub-surface cycling of sulfur and iron, decreased dissolved sulfide and increased dissolved iron concentrations, the mechanisms which produced these results differed dramatically.

Keywords: redox cycling, sulfate reduction, porewater chemistry, bioturbation, *Spartina alterniflora*, tropical seagrasses

INTRODUCTION

Plants and animals that live in or on sedimentary environments have considerable influence on the physical and chemical conditions of these sediments. Animals affect sediments by particle mixing due to movements during foraging for food or escaping from prey (Whitlatch, 1974; Cadée, 1976; Tevesz et al., 1980) or by the ingestion of particles during feeding and the transport of those particles to the sediment surface during defecation (Rhoads, 1967; Cadée, 1979; Taghon et al., 1984). Fecal pellets may be buried rapidly by new pellets as they are deposited at the surface.

Animals also influence sediments through irrigation of burrows (Aller et al.,

1983). Both reworking and irrigation activities can have a profound effect on the microbiology of the sediments by transporting fresh organic matter to depth (Aller and Yingst, 1980, Hines and Jones, 1985), breaking down aggregates which can be colonized by microbes (Lopez and Levinton, 1978), transferring reduced compounds to oxidizing regions (Rhoads, 1974; Hines and Jones, 1985), and removing toxic metabolites while providing nutrients (Hargrave, 1970; Aller, 1977). Bioturbation has been reported to enhance rates of nitrification and denitrification (Sayama and Kurihara, 1978); Kristensen et al., 1985), SO_4^{2-} reduction (Aller and Yingst, 1980; Hines and Jones, 1985) and ammonification (Aller and Yingst, 1980).

Bioturbation affects sedimentary chemistry by disrupting vertical zonations of biogeochemical processes (Aller, 1977, 1982; Aller and Yingst, 1985). This results in redox gradients which may be situated horizontally and vertically as in the case of vertical, oxygenated burrows or more randomly as in microenvironments such as fecal pellets (Aller, 1977, 1982; Jørgensen, 1977). In general, the enhanced mixing of overlying water and porewater lowers the concentrations of most solutes in sediments. However, redox sensitive elements which change phases when reduced or oxidized may display increased porewater concentrations as a result of infaunal activity and subsurface redox cycling (Goldhaber et al., 1977; Hines et al., 1982, 1984).

Vascular plants such as marsh grasses and seagrasses can affect sedimentary chemistry in a manner which is similar to the effects of infauna. Although these organisms are not capable of particle movement, they influence the sediments by actively or indirectly transporting solutes and gases to the root zone (Wetzel and Penhale, 1979; Howes et al., 1981; Mendelssohn et al., 1981). In addition, rapid production by these plants can provide a subsurface source of organic matter to fuel microbial activity. Therefore, rapid subsurface redox cycles such as those in bioturbated sediments may be prevalent in sediments inhabited by active plant communities. The present communication compares sedimentary redox cycling in sediments subjected to active bioturbation by a subsurface deposit-feeding polychaete to temperate sediments inhabited by the salt marsh grass *Spartina alterniflora* and to tropical sediments inhabited by a variety of seagrasses. The net effect of the activities of these fauna and flora were similar, i.e., enhancement of sub-

surface anaerobic microbial activity, movement of oxidants to depth in the sediments and a rapid subsurface redox cycle of S and Fe. However, the infauna produced these events by transporting solid phase organic matter and oxidants into the sediment while the flora transported dissolved organic matter and molecular oxygen or dissolved oxidants.

MATERIALS AND METHODS

Sample locations

Bioturbated Site. Subtidal sediments in a shallow area of Great Bay, New Hampshire, U.S.A., were studied for several years. This site, which has been described by Hines and Jones (1985), is located just below the low tide mark in a -0.7 ha cove. Mean tidal range is -2 m and the temperature ranges from -0.5 to 25°C. The sediments are predominantly silts and clays with a large percentage of organic aggregates (Winston and Anderson, 1971). Cores collected for a 13 month period between 1984 and 1986 were examined for macroorganism content by P.F. Larsen (Bigelow Laboratory for Ocean Sciences, unpublished data) and revealed that the majority of the biomass in these sediments was attributable to the subsurface deposit-feeding polychaete *Heteromastus filiformis*. During summer, this organism reached population sizes as high as -5000 individuals m⁻². Other infaunal species (36 total) were abundant but very small and restricted to the upper 1-2 cm of the sediment.

Salt Marsh Site. Chapman's Marsh is located near the mouth of the Squamscott River in the upper regions of Great Bay, New Hampshire and is described in detail

in Hines et al. (in review). This marsh is dominated by *Spartina patens* with stands of *S. alterniflora* along creek and river banks. Because of the steep slope of the banks the *S. alterniflora*-inhabited areas are generally less than 30 m wide and in some locations are only a few meters in width. The area sampled contained the tall form of *S. alterniflora* which reached over 2 m in height. The transition from tall to short *S. alterniflora* is abrupt and the tall *S. alterniflora* occupies a major percentage of the total *S. alterniflora*-containing soils. The tidal range at the marsh is ~2 m. The soil contained relatively fine grained mineral matter in addition to root and rhizome material.

Tropical Seagrass Site. Samples were collected from a shallow water site near the NE end of San Salvador Island, Bahamas. This location is described in Short et al. (1985). The sediments contained relatively fine-grained carbonate material and were inhabited by nearly pure seagrass stands of either *Thalassia testudinum*, *Syringodium filiforme*, or *Halodule wrightii* and sediment samples were collected from all three grasses. In addition, sediment samples were collected from a control site with no live seagrasses but with abundant remnants of seagrass roots and rhizomes. This control area was more affected by wave wash than in the vegetated areas.

Sample Collection. Sediment cores from the bioturbated site were collected using a hand-held plexiglas box corer (Hines and Jones, 1985). These were transported to the laboratory with the overlying water in place. Cores from the marsh site were collected using a Wildco corer which contained a plastic core liner and core catcher. Cores

were flushed immediately in the field with N_2 and transported to the laboratory. Cores from the Bahamas sites were collected by hand using polycarbonate core liners. These latter samples were distributed into vessels in the field.

Porewaters from the bioturbated site were collected by centrifuging sediment horizons and filtering the supernatant under N_2 (Hines et al., 1984). Porewaters from both the marsh and tropical sites were collected using *in situ* "sippers" as described in Short et al. (1985) and Hines et al. (in review). These devices, which are deployed several days to weeks in advance of use, are lysimeters made of teflon which contain a porous teflon collar at the desired depth for water collection. Porewater is drawn into the sipper by application of a vacuum under N_2 . Samples are immediately filtered under N_2 in the field and divided into storage vessels anoxically. Sippers are necessary to prevent artifacts due to the destruction of roots during sampling (Howes et al., 1985).

Sulfate Reduction Rates. Rates of sulfate reduction were determined using ^{35}S according to Jørgensen (1978) as modified by Westrich (1983). Sediment samples were placed into 5 cc syringes which were sealed with serum stoppers. One μCi of $^{35}S-SO_4^{-2}$ was injected into each syringe and samples were incubated in a dark N_2 -filled jar overnight at ambient temperature. Activity was stopped by freezing. Sulfur-35 present in acid-volatile sulfides (AVS) was determined by actively distilling sulfides into Zn acetate traps as described by Hines and Jones (1985). Chromium-reducible sulfur-35, which represents largely pyrite and elemental sulfur, was determined by reducing these species to sulfide by refluxing with acidified Chromium (II) (Zhabina and

Volkov, 1978; Westrich, 1983). Only the AVS portion was determined in the bioturbated sediments.

Porewater Analyses. Sulfide was measured colorimetrically according to Cline (1969). Dissolved iron was determined colorimetrically using FerroZine (Stookey, 1970). Sulfate was determined turbidimetrically (Tabatabai, 1974).

RESULTS

Bioturbated site

Relative changes in bioturbation were determined using X-radiographs, abundances of infauna, and changes in sedimentary chemistry. In general, the influence of infaunal activity on sedimentary chemistry commenced in June during most years and was accompanied by an increase in rates of SO_4^{2-} reduction, an increase in the concentration of dissolved Fe, and a decrease in HS^- (Hines et al., 1984, 1985). Figure 1 demonstrates that dissolved Fe was abundant in JEL sediments throughout sedimentary regions that experienced relatively rapid rates of SO_4^{2-} reduction. Dissolved sulfide was never detected (detection limit 1–2 μM) in the upper 8–10 cm during the summers in which bioturbation was observed even though HS^- production increased to maximal levels during this time (Hines et al., 1985). The variations in dissolved Fe depicted in Fig. 1 were probably present at very low levels in these sediments but was maintained at undetectable concentrations by its rapid removal by FeS precipitation. The highest concentrations of dissolved Fe always occurred during the summer. For comparison, a relatively non-bioturbated site in Great Bay did not dis-

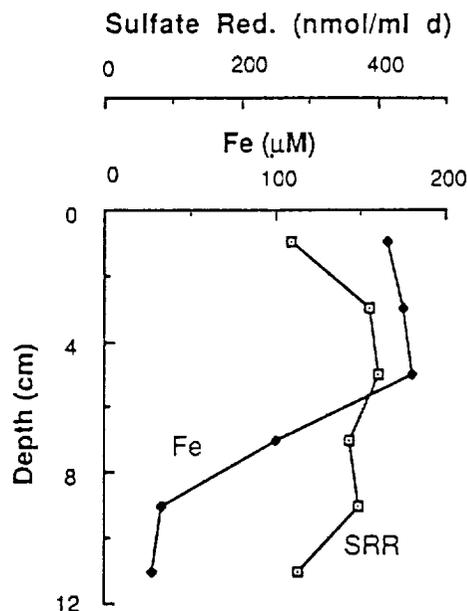


Fig. 1. Typical depth profile of dissolved Fe and rates of sulfate reduction (SRR) in the bioturbated sediments during summer. Dissolved sulfide concentrations were below detection ($< 2.0 \mu\text{M}$).

play an increase in dissolved Fe during the summer and rates of SO_4^{2-} reduction were much slower than at the bioturbated location (Hines and Jones, 1985).

Salt marsh site

Above-ground plant growth in the marsh soils studied began in mid-June and elongation ceased once the plants flowered in early August. Sulfate reduction was very rapid in the marsh soils and rates displayed sharp maxima when plants were actively elongating (Fig. 2). Once the *S. alterniflora* flowered, SO_4^{2-} reduction decreased ~4-fold within a few days. Temporal changes in SO_4^{2-} reduction rates agreed well with changes in $\text{SO}_4^{2-}/\text{Cl}$ ratios (data not shown). However, as pointed out by Hines et al. (in review), $\text{SO}_4^{2-}/\text{Cl}$ ratios in these

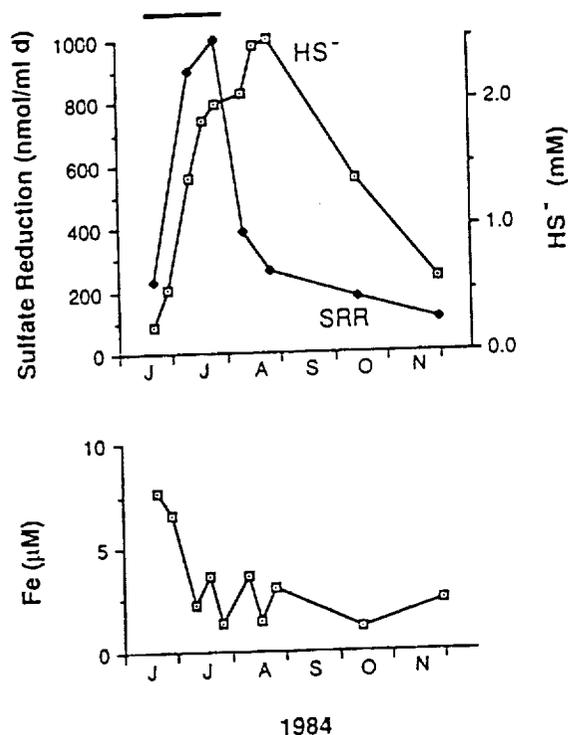


Fig. 2. Temporal variations in sulfate reduction rate (SRR) and concentrations of dissolved sulfide (HS^-) and dissolved Fe in the salt marsh sediments inhabited by the tall form of *Spartina alterniflora*. Values represent averages of upper 20 cm of sediment. Bar represents period when plants were actively elongating above ground. The detection limit for dissolved Fe was $\sim 0.2 \mu\text{M}$.

marsh sediments can only be used qualitatively because of the influence of vertical and lateral groundwater movement and the oxidation of the soils by plant activity.

Dissolved sulfide concentrations increased as plant height and rates of SO_4^{2-} reduction increased (Fig. 2). Concentrations of HS^- began to level near the end of the active elongation period. After *S. alterniflora* flowered in August, the concentrations of HS^- increased rapidly again even though rates of HS^- production had decreased dramatically. These concentrations decreased again in the Fall.

Dissolved Fe concentrations were low in these sediments when plants were elongating and decreased throughout the summer (Fig. 2). However, Fe was always detectable in the porewaters despite the occurrence of mM levels of HS^- .

Tropical seagrass beds

Sulfate reduction rates were ~ 10 -fold lower in the sediments inhabited by seagrasses compared to the marsh soils described above (Fig. 3). Rates were most rapid in sediments occupied by *Halodule*, and slowest in sediments inhabited by *Thalassia*. Concentrations of HS^- were very low in the control sediments but reached values > 1 mM in seagrass sediments. The highest HS^- concentrations occurred in the *Syringodium* beds while concentrations were very low in the sediments inhabited by *Halodule*. Iron was not measured in these porewaters but presumably Fe concentrations were very low due to the carbonate composition of the island and of the sediments and the fact that this island is on the outer bank of the Bahamian islands.

There was no detectable decrease in SO_4^{2-} with depth in any of the tropical sediments examined (data not shown). This lack of SO_4^{2-} depletion has been noted in other carbonate sediments which exhibit SO_4^{2-} reduction which is even more rapid than rates noted for these Bahamian sediments (Hines and Lyons, 1982; Hines, 1985).

DISCUSSION

The production rates of HS^- (SO_4^{2-} reduction) in the bioturbated sediments in Great Bay were highest during the summer when temperatures were high and the sedi-

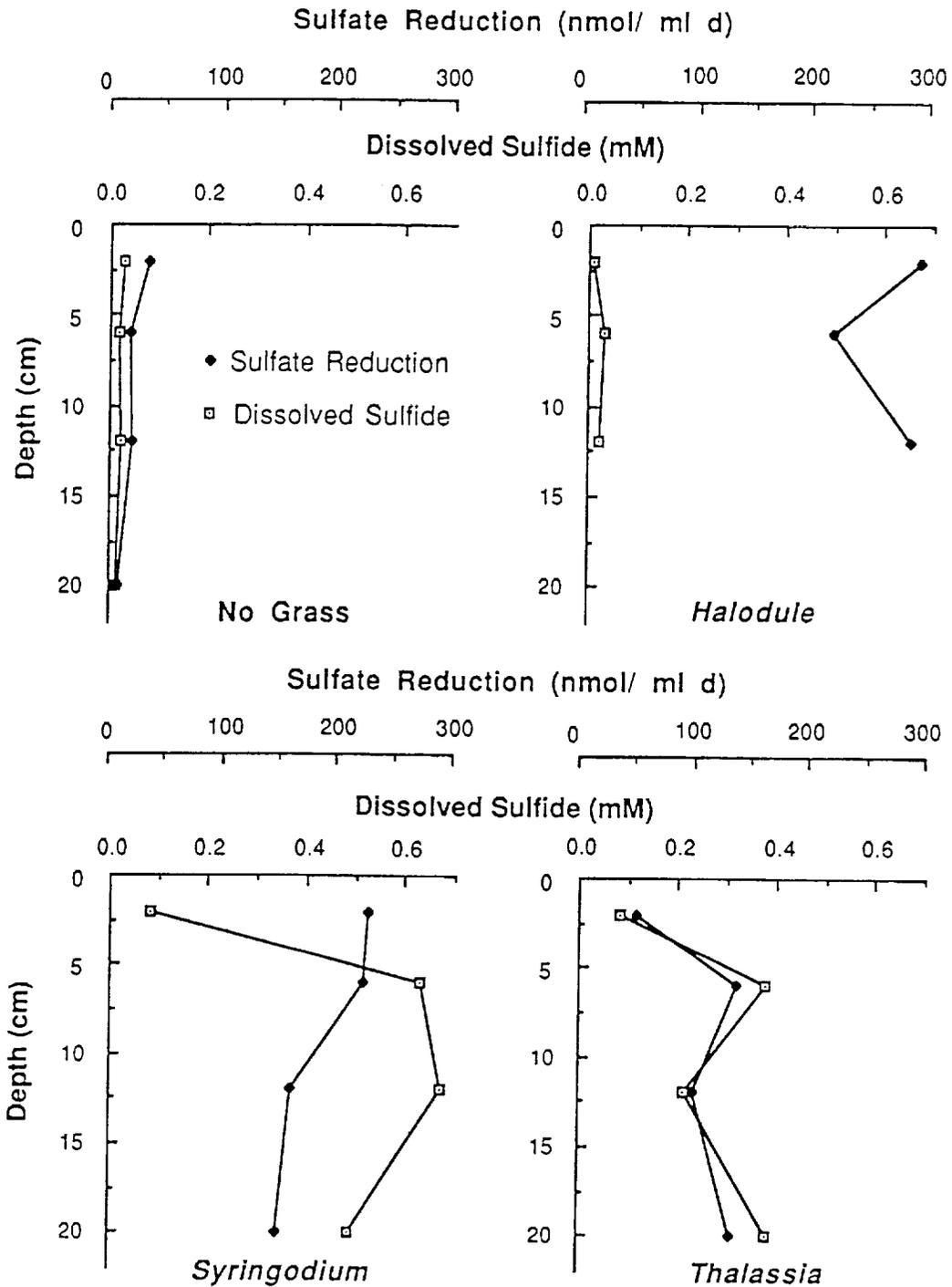


Fig. 3. Depth profiles of sulfate reduction rates and dissolved sulfide concentrations in various carbonate sediments from the Bahamas.

ments were subjected to active bioturbation (Hines and Jones, 1985). However, during this time of year, dissolved Fe was at maximal concentrations and HS^- concentrations were low or undetectable in the porewaters (Fig. 1). Although some Fe may have been complexed by organosulfur ligands (Boulegue et al., 1982), Fe cannot remain in solution at high concentrations in the presence of HS^- production since in anoxic sulfidic sediments the concentration of dissolved Fe is controlled primarily by the precipitation of Fe sulfide minerals (Lyons, 1979). To maintain high concentrations of dissolved Fe in these sediments which were experiencing rapid rates of HS^- production, it was necessary that the appropriate oxidants were continuously supplied to fuel a subsurface redox cycle of Fe and S which would result in the reduction and dissolution of Fe (Hines et al., 1982). Hence, Fe(III) had to be introduced into the sediments and reduced to Fe(II) at a rate which was at least fast enough to remove HS^- as it was generated microbially. One mechanism for providing the appropriate oxidant would be the introduction of O_2 into the sediments via burrow irrigation. However, a more plausible mechanism for the sediments studied here can be deduced from an examination of the lifestyle of the predominant bioturbator.

The infaunal community at JEL is dominated on a biomass basis by the subsurface deposit-feeding polychaete *H. filiformis*. This organism is a classic "conveyor-belt" feeder (Rhoads, 1974) which consumes fine anoxic sediment at 8–30 cm and passes it, through its gut, to the surface without oxidizing the reduced material (Cadée, 1979). Often, the fecal pellets are black (FeS) when deposited and they are then oxidized at the sediment surface (Cadée,

1979). The burrows are not ventilated and are not surrounded by a zone of oxidation (Pals and Pauptit, 1979). The worm is adapted physiologically to life in O_2 -deficient environments (Pals and Pauptit, 1979).

The movement of fecal pellets by *H. filiformis* supplied the necessary oxidants to drive a subsurface redox cycle in the sediments studied. Reduced sediment in fecal material was oxidized at the sediment surface chemically and/or biologically. Additional pellet production buried the oxidized pellets into anoxic regions where they were reduced chemically and/or biologically, thus allowing for the dissolution of Fe. The Fe(II) produced was available for removing HS^- as FeS and HS^- never accumulated in the porewaters. In this way, a complete redox cycle of Fe and S occurred in deeper sediments without the need for the introduction of molecular O_2 into the sediments. Although particle reworking rates were not measured in these sediments, the population size of *H. filiformis* was sufficient to turn over the upper 10–15 cm of sediment several times during the summer (Cadée, 1979; Shaffer, 1983).

If the reduction of Fe(III) occurred chemically during HS^- oxidation then the production of FeS required two moles of HS^- for each mole of Fe since one mole of HS^- would have been consumed during the reduction of Fe(III). If Fe reduction was due to the use of Fe as an electron acceptor by bacteria then FeS precipitation required only one mole each of Fe and HS^- . Iron-reducing bacteria have been isolated from these sediments but the extent of Fe reduction that is strictly biological is unknown (Tugel et al., 1986).

The marsh and seagrasses studied also affected the subsurface redox chemistry in the sediments. One major difference be-

TABLE 1

Calculated resident times (days) of dissolved sulfide in the various sediments studied. Values equal the quotient of the concentration of sulfide divided by the rate of sulfate reduction

Bioturbated site	Marsh sediments		Tropical sediments			
	During growth	After flowering	<i>Halodule</i>	<i>Syringodium</i>	<i>Thalassia</i>	control
<.0067	1.5-2.0	5.1-10	0.16	2.7	2.4	1.2

tween the effects of bioturbation in Great Bay and the effects of the vascular plants was that the infaunal activities resulted in the complete removal of HS^- from solution while considerable HS^- remained in the plant inhabited porewaters. However, comparisons of the HS^- concentrations and rates of SO_4^{2-} reduction in the grass-inhabited areas revealed that plant activity had a strong influence on the redox chemistry of S in the sediments. The turnover time or residence time of HS^- in the porewaters was calculated by dividing the HS^- concentration by the rate of HS^- production or SO_4^{2-} reduction (Table 1). Since the rate measurements represent a value for the incubation period only and the concentration values are the result of previous and ongoing activity in the sediments, this calculation represents only an approximation of the reactivity of HS^- in the sediments. However, the wide range in values in Table 1 gives credence to use of these calculations for estimating the effect of the macroorganisms on S transformations.

Sulfide was not detected in the porewaters at the bioturbated site during summer so the HS^- residence times were calculated by using the detection limit of the method which is $2 \mu\text{M}$ ($1 \mu\text{mol}^{-1}$ whole sediment at 50% porosity). Therefore, the residence time of HS^- during bioturbation was <10 min. This value represents removal of

HS^- by all mechanisms and is not necessarily a measure of HS^- oxidation.

Although the HS^- concentrations in the marsh porewaters were high, the highest concentrations were encountered after SO_4^{2-} reduction had decreased greatly. Therefore, the calculations of HS^- residence times revealed a nearly 10-fold increase after the plants flowered (Table 1). The onset of flowering produced dramatic changes in the biogeochemistry of the soils including a ~4-fold decrease in SO_4^{2-} reduction and an increase in HS^- concentrations. The fact that the residence time of HS^- in the porewaters increased rapidly after flowering and was similar to values measured after the growing season ended (Table 1) demonstrated that the plants were able to oxidize the soils significantly only when they were elongating actively above ground. Although it was not clear whether the plant-mediated oxidation of the soil was due to molecular O_2 or to some other oxidized chemical species produced biochemically (Howes et al., 1981), it seems certain that the oxidizing agent was dissolved as opposed to the solid phase oxidant present in the bioturbated sediments at JEL. The possibility of O_2 as the oxidant in *Spartina* marshes has been discussed by Boulegue et al. (1982). Even though a decrease in residence time of HS^- does not indicate that HS^- is being removed ex-

clusively by oxidation in the soil, the introduction of an oxidizing agent is required to continually remove HS^- whether removal occurs via oxidation or precipitation as an Fe mineral.

The result of sediment oxidation by the *S. alterniflora* was not as apparent as that noted for the bioturbated sediments. However, the enhancement of SO_4^{2-} reduction by the plant was dramatic. The rapid increase in SO_4^{2-} reduction that occurred when plants were elongating above ground could not have been due to the utilization of solid phase organic matter. It was likely that dissolved organic exudates produced by the plants (Mendelssohn et al., 1981) were responsible for fueling the majority of SO_4^{2-} reduction. The "background" rates of $\sim 200\text{--}300 \text{ nmol ml}^{-1} \text{ d}^{-1}$ which occurred before and after the occurrence of the SO_4^{2-} reduction maximum were probably due to the utilization of this solid phase material. Therefore, in contrast to the bioturbated sediments, when the plants were elongating, anaerobic microbial activity was fueled primarily by dissolved organic matter and

the subsurface redox cycle was sustained by the production of dissolved oxidants.

The residence time of HS^- in the tropical seagrass-inhabited sediments were similar to those in the marsh soils. However, the rates of SO_4^{2-} reduction and the concentrations of HS^- were considerably less than in the marsh soils. *Halodule* tended to oxidize the soils much more than did the other grasses. In fact, these sediments were the only ones which yielded HS^- residence time data which were more rapid than the control. It was difficult to compare residence time data to the control since the low level of HS^- and SO_4^{2-} reduction in the control probably increased the importance of diffusional losses and oxidation in control sediments. The wave activity at the control site may have enhanced HS^- removal as well. A better control would have been obtained if vegetated areas had been cut to prevent photosynthesis. The enhancement of sediment oxidation in seagrass-inhabited sediments was most likely due to dissolved oxidants as in the marsh soils. Sulfate reduction was also most rapid in the sediments inhabited

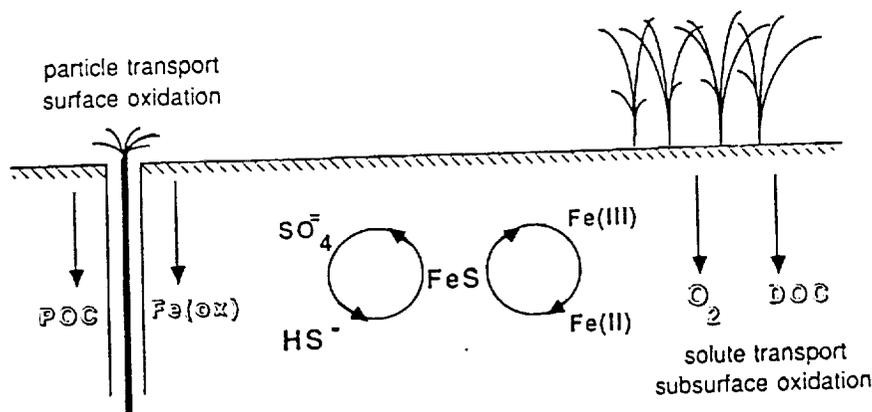


Fig. 4. Summary of the net result of bioturbation and plant activities on the redox conditions of the marine sediments studied. Both types of macroorganisms cause subsurface redox cycling but the mechanisms utilized are different.

by *Halodule* which may indicate that this species is active at providing oxidants and organic exudates to the sediments. Wetzel and Penhale (1979) demonstrated the capacity of seagrasses to release organic exudates from the root zone. However, the data from these Bahamian sediments were insufficient to determine whether SO_4^{2-} reduction was fueled primarily by dissolved (DOC) or particulate (POC) organic matter.

The net result of the occupation of the marine sediments studied by either infauna or flora was an enhancement of anaerobic microbial activity measured as sulfate reduction and the establishment of a subsurface redox cycle which caused high dissolved Fe and low HS^- concentrations. This process and the mechanisms by which these organisms produced these changes are summarized in Figure 4. The deposit-feeding polychaete community provided solid phase organic matter and oxidized Fe to subsurface sediments and were efficient at removing HS^- . Conversely, the flora studied enhanced anaerobic activity and maintained a subsurface redox cycle by providing dissolved organic matter and dissolved oxidants to the sediments. These HS^- removal mechanisms may be important for maintaining HS^- concentrations below levels which are toxic to macroorganisms.

ACKNOWLEDGEMENTS

The assistance of J. Tugel, S. Knollmeyer, M. Spencer, B. Lyons, A. Eldredge, D. Luken, F. Short, E. Brainard, D. Capone and the crew of the R.V. Calanus is gratefully acknowledged. I especially appreciate the discussions with P. Larsen and the use of his unpublished data. Financial support was provided by National Science Founda-

tion grants OCE-80-18460, OCE-82-14863 and OCE-85-15639, and National Aeronautics and Space Administration grant NAGW-512.

REFERENCES

- Aller, R.C., 1977. The influence of macrobenthos on chemical diagenesis of marine sediments. Ph.D. thesis, Yale Univ., New Haven.
- Aller, R.C., 1982. The effects of macrobenthos on chemical properties of marine sediment and the overlying water. Un: O.L. McCall and M.J.S. Tevesz (Editors), *Animal-Sediment Relations*. Plenum Press, New York. pp. 53-102.
- Aller, R.C. and J.Y. Yingst. 1980. Relationships between microbial distributions and the anaerobic decomposition of organic matter in surface sediments of Long Island Sound, USA. *Mar. Biol.*, 56:29-42.
- Aller, R.C. and J.Y. Yingst, 1985. Effects of the marine deposit-feeders *Heteromastus filiformis* (Polychaeta), *Macoma balthica* (Bivalvia), and *Telling texana* (Bivalvia) on averaged sedimentary solute transport, reaction rates, and microbial distribution. *J. Mar. Res.*, 43:615-645.
- Aller, R.C., J.Y. Yingst and W.J. Ullman, 1983. Comparative biogeochemistry of water in intertidal *Onuphis* (Polychaeta) and *Upogebia* (Crustacea) burrows: temporal patterns and causes. *J. Mar. Res.*, 41:571-604.
- Boulegue, J., C.J. Lord and T.M. Church, 1982. Sulfur speciation and associated trace metals (Fe, Cu) in the pore waters of Great Marsh, Delaware. *Geochim. Cosmochim. Acta*, 46:453-464.
- Cadée, G.C., 1976. Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.*, 10:440-460.
- Cadée, G.C., 1979. Sediment reworking by the polychaete *Heteromastus filiformis* on a tidal flat in the Dutch Wadden Sea. *Neth. J. Sea Res.*, 13:441-456.
- Cline, J.D., 1969. Spectrophotometric determination of hydrogen sulfide in natural waters. *Limnol. Oceanogr.*, 14:454-458.
- Goldhaber, M.B., R.C. Aller, J.K. Cochran, J.K. Rosenfeld, C.S. Martens and R.A. Berner, 1977. Sulfate reduction, diffusion and bioturbation in Long Island Sound sediments: Report of the FOAM group. *Amer. J. Sci.*, 227:193-227.
- Hargrave, B.T., 1970. The effect of a deposit-feeding amphipod on the metabolism of benthic microflora. *Limnol. Oceanogr.*, 15:21-30.

- Hines, M.E., 1985. Microbial biogeochemistry in shallow water sediments of Bermuda. Proceedings, Fifth International Coral Reef Congress, 3:427-432.
- Hines, M.E. and G.E. Jones, 1985. Microbial biogeochemistry in the sediments of Great Bay, New Hampshire. Estuar. Coast. Shelf Sci., 20:729-742.
- Hines, M.E., S.L. Knollmeyer and J.B. Tugel. Sulfate reduction and sedimentary biogeochemistry in a Northern New England salt marsh. In review.
- Hines, M.E. and W.B. Lyons, 1982. Biogeochemistry of nearshore Bermuda sediments. I. Sulfate reduction rates and nutrient generation. Mar. Ecol. Prog. Ser., 8:87-94.
- Hines, M.E., W.B. Lyons, P.B. Armstrong, W.H. Orem, M.J. Spencer and H.E. Gaudette, 1984. Seasonal metal remobilization in the sediments of Great Bay, New Hampshire. Mar. Chem., 15:173-187.
- Hines, M.E., W.H. Orem, W.B. Lyons and G.E. Jones, 1982. Microbial activity and bioturbation-induced oscillations in pore water chemistry of estuarine sediments in spring. Nature, 299:433-435.
- Hines, M.E., M.J. Spencer, J.B. Tugel, W.B. Lyons and G.E. Jones, 1985. Seasonal sulfate reduction and iron mobilization in estuarine sediments. In: D. Caldwell, J.A. Brierley and C.L. Brierley (Editors), Planetary Ecology. Van Nostrand Reinhold, New York. pp. 222-229.
- Howes, B.L., J.W.H. Dacey and S.G. Wakeham, 1985. Effects of sampling technique on measurements of porewater constituents in salt marsh sediments. Limnol. Oceanogr., 30:221-227.
- Howes, B.L., R.W. Howarth, J.M. Teal and I. Valiela, 1981. Oxidation-reduction potentials in a salt marsh: Spatial patterns and interactions with primary production. Limnol. Oceanogr., 26:350-360.
- Jørgensen, B.B., 1977. Bacterial sulfate reduction within reduced microniches of oxidized marine sediments. Mar. Biol., 41:7-17.
- Jørgensen, B.B., 1978. A comparison of methods for the quantification of bacterial sulfate reduction in coastal marine sediments. I. Measurements with radiotracer techniques. Geomicrobiol. J., 1:11-27.
- Kristensen, E. M.H. Jensen and T.K. Andersen, 1985. The impact of polychaete *Nereis virens* (Sars) burrows on nitrification and nitrate reduction in estuarine sediments. J. Exp. Mar. Biol. Ecol., 85:75-91.
- Lopez, G.R. and J.S. Levinton, 1978. The availability of microorganisms attached to sediment particles as food for *Hydrobia ventrosa* Montagu (Gastropoda: Prosobranchia). Oecologia (Berl.), 32:263-275.
- Lyons, W.B., 1979. Early diagenesis of trace metals in nearshore Long Island Sound sediments. Ph. D. thesis, Univ. Connecticut, Storrs.
- Mendelssohn, I.A., K.L. McKee and W.H. Patrick, Jr., 1981. Oxygen deficiency in *Spartina alterniflora* roots: Metabolic adaptation to anoxia. Science, 214:439-441.
- Pals, G. and E. Pauptit, 1979. Oxygen binding properties of the coelomic haemoglobin of the polychaete *Heteromastus filiformis* related with some environmental factors. Neth. J. Sea Res., 13:581-592.
- Rhoads, D.C., 1967. Biogenic reworking of intertidal and subtidal sediments in Barstable Harbor and Buzzards Bay, Massachusetts. J. Geol., 10:461-476.
- Rhoads, D.C., 1974. Organism-sediment relations on the muddy seafloor. Ann. Rev. Mar. Biol., 12:263-300.
- Sayama, M. and Y. Kurihara, 1978. Relationship between burrowing activity of the polychaetous annelid, *Neanthes japonica* (Izuka) and nitrification-denitrification processes in the sediments. J. Exp. Mar. Biol. Ecol., 72:233-241.
- Shaffer, P.L., 1983. Population ecology of *Heteromastus filiformis* (Polychaeta; Capitellidae). Neth. J. Sea Res., 17:106-125.
- Short, F.T., M.W. Davis, R.A. Gibson and C.F. Zimmerman, 1985. Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. Estuar. Coast. Shelf Sci., 20:419-430.
- Stokey, L.L., 1970. FerroZine — A new spectrophotometric reagent for iron. Anal. Chem., 42:779-781.
- Tabatabai, M.A., 1974. Determination of sulfate in water samples. Sulfur Inst. J., 10:11-13.
- Taghon, G.L., A.R.M. Nowell and P.A. Jumars, 1984. Transport and breakdown of fecal pellets: Biological and sedimentological consequences. Limnol. Oceanogr., 29:64-72.
- Tevesz, M.J.S., F.M. Soster and P.L. McCall, 1980. The effects of size selective feeding by oligochaetes in the physical properties of river sediments. J. Sed. Petrol., 50:561-568.
- Tugel, J.B., M.E. Hines and G.E. Jones, 1986. Microbial iron reduction by enrichment cultures isolated from estuarine sediments. Appl. Environ. Microbiol., 52:1167-1172.
- Westrich, J.T., 1983. The consequences and control of bacterial sulfate reduction in marine sediments. Ph.D. thesis, Yale Univ., New Haven.
- Wetzel, J.T. and P.A. Penhale, 1979. Transport of carbon and excretion of dissolved organic carbon by leaves and root rhizomes in seagrass and their epiphytes. Aquat. Bot., 6:149-158.

- Whitlatch, R.B., 1974. Food-resource partitioning in the deposit-feeding polychaete *Pectinaria gouldii*. Biol. Bull., 147:227-235.
- Winston, J.E. and F.E. Anderson, 1971. Bioturbation of sediments in a northern temperate estuary. Mar. Geol., 10:39-49.
- Zhabina, N.N. and I.I. Volkov, 1978. A method of determination of various sulfur compounds in sea sediments and rocks. In: Environmental Biogeochemistry and Geomicrobiology, Vol. 3, Proc. 3rd Int. Symp., Ann Arbor Sci., p. 735-746.